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Research Article

Host plants of the weevil genus *Heilipus* Germar, 1824 (Coleoptera, Curculionidae, Molytinae, Molytini, Hylobiina)

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Abstract

Heilipus Germar, 1824 (Coleoptera, Curculionidae, Molytinae, Molytini, Hylobiina) is a largely understudied tropical lineage of weevils with 90 described species distributed from the southern United States to northern Argentina. Several of its species cause damage to avocado (*Persea americana* Mill.; Lauraceae Juss.) crops in the Americas. Apart from the species of economic importance, there is a paucity of information regarding the host plants of species of *Heilipus*. This study presents a comprehensive overview of the current knowledge on the habits and host plants of this group of weevils, based on a literature review and the examination of label data associated with entomological material in museums and scientific collections. The larval stages of 24 *Heilipus* species are borers of either seeds or trunks of 38 plant species belonging to 13 genera: 33 species (12 genera) from the family Lauraceae and five species (one genus) from the family Annonaceae Juss. Four new host plant records and the first identification of habits and host plants for *H. albovenosus* (Champion), *H. empiricus* (Pascoe), *H. fassli* (Voss) and *H. mirus* (Pascoe) are provided. The biology and host plants of the seed and trunk borers are discussed, as well as the oligophagous feeding behaviour exhibited by these two feeding guilds. Seed-boring *Heilipus* species constitute one of the primary groups of pre-dispersal seed predators of the family Lauraceae in the Americas. Furthermore, the high diversity of *Heilipus* and its host plants in the Brazilian Atlantic Forest suggests that this area may be a possible centre of origin for these weevils.

Resumen

Heilipus Germar, 1824 (Coleoptera, Curculionidae, Molytinae, Molytini, Hylobiina) es un linaje tropical de picudos poco estudiado, con 90 especies descritas distribuidas desde el sur de Estados Unidos hasta el norte de Argentina. Varias de sus especies causan daños en cultivos de aguacate (*Persea americana* Mill.; Lauraceae Juss.) en las Américas. Aparte de las especies de importancia económica, hay escasez de información sobre las plantas hospedantes de las especies de *Heilipus*. Este estudio presenta una visión integral del conocimiento actual sobre los hábitos y plantas hospedantes de este grupo de gorgojos, basada en la revisión de literatura y el examen de datos de etiquetas asociadas con material entomológico en museos y colecciones científicas. Los estados larvarios de 24 especies de *Heilipus* son barrenadores de semillas o troncos de 38 especies de plantas pertenecientes a 13 géneros: 33 especies (12 géneros) de la familia Lauraceae y cinco especies (un género) de la familia Annonaceae Juss. Se proporcionan cuatro nuevos registros de plantas hospedantes y la primera identificación de hábitos y plantas hospedantes para *H. albovenosus* (Champion),

H. empiricus (Pascoe), *H. fassli* (Voss) y *H. mirus* (Pascoe). Se discuten la biología y plantas hospedantes de los barrenadores de semillas y de troncos, así como el comportamiento alimentario oligófago exhibido por estos dos gremios de alimentación. Las especies de *Heilipus* barrenadoras de semillas constituyen uno de los principales grupos de depredadores de semillas pre-dispersión de la familia Lauraceae en las Américas. Además, la alta diversidad de *Heilipus* y sus plantas hospedantes en la Mata Atlántica brasileña sugiere que esta área puede ser un posible centro de origen de estos gorgojos.

Key Words

Annonaceae, avocado, Lauraceae, oligophagy, pre-dispersal seed predators, trunk borers

Palabras clave

Annonaceae, aguacate, Lauraceae, oligofagia, depredadores de semillas pre-dispersión, barrenadores de troncos

Introduction

The weevil genus *Heilipus* (Coleoptera, Curculionidae, Molytinae, Molytini, Hylobiina) (Fig. 1) was described by Germar in 1824. According to Kuschel (1955), the diagnostic characters of the genus include a glabrous prementum, curved hind tibia ending in a strong unciform mucro at the inner angle, absent premucro and a tuberculiform mesosternal process. *Heilipus* currently comprises 90 described species distributed across the Americas, from the southern United States to northern Argentina (Anzaldo and Díaz-Grisales 2022; Sanz-Veiga et al. 2024). Species of this genus cause damage to avocado crops (*Persea americana* Mill; Laurales, Lauraceae Juss.) (Castañeda-Vildózola et al. 2013). As of 2019, nine of the 90 described species had been reported on avocado seeds and trunks (Castañeda-Vildózola et al. 2013; Díaz-Grisales 2019), highlighting *Heilipus* as one of the most important groups of phytophagous insects for this crop in the Americas (Lourenção et al. 2003; Castañeda-Vildózola et al. 2007). Despite its economic importance, the genus has been poorly studied (Lourenção et al. 2003; Morrone 2003; Rubio et al. 2009). There is neither an identification key to the species nor a formal taxonomic revision for the genus. Furthermore, the phylogenetic relationships within the group have never been studied. Another significant gap in our knowledge of *Heilipus* relates to the host plants (Lourenção et al. 2003; Rubio et al. 2009). Aside from the nine species associated with avocado, the habits and host plants of only 11 other species are known.

The life histories of *Heilipus* species vary. Some species oviposit within fruits and their larvae feed on the seeds of the host plant (spermophagous) (Fig. 1A–D). Others deposit their eggs on the bark of trunks and branches (Fig. 1E–H), with larval feeding and development occurring in the subcortical plant tissues (Fig. 1E) (Silva et al. 1968; Castañeda-Vildózola et al. 2013; Díaz-Grisales et al. 2021). The first mention of a host plant for the genus *Heilipus* was likely made by the Swedish entomologist Carl H. Boheman in his original description of *Heilipus lauri* (Fig. 1D) (Schoenherr 1845). Boheman stated that the type specimen of *H. lauri* was from Mexico and that its metamorphosis occurred in a fruit of "*Lauri drymifoliae*". The species mentioned by Boheman is likely the one currently known as *Persea drymifolia* Schltdl. & Cham., the basionym of *Persea americana* var. *drymifolia* (Schltdl. & Cham.) S.F. Blake (Missouri Botanical Garden 2024), the Mexican race of avocado or Mexican criollo avocado. The association of *H. lauri* with avocado seeds (Fig. 1C) was later confirmed by Champion (1902) and Barber (1912, 1919). Similarly, studies of avocado crops in the Americas enabled the identification of two additional seed borers, *H. trifasciatus* (Fabricius) and *H. pittieri* Barber, as well as the trunk borers *H. albopictus* (Champion) (Fig. 1E, F) (Castañeda-Vildózola et al. 2010), *H. catagraphus* Germar (Bondar 1915; Costa-Lima 1956; Silva et al. 1968), *H. elegans* Guérin (Rubio et al. 2009), *H. leopardus* Boheman (Díaz-Grisales 2019), *H. rufipes* Perty (Lourenção et al. 2003) and *H. squamosus* (LeConte) (Fig. 1H) (Wolfenbarger 1948).

In addition to the genus *Persea* Mill., *Heilipus* species have been recorded in other genera of the family Lauraceae and in the genus *Annona* L. (Magnoliales, Annonaceae Juss.). Records in Lauraceae include seed and trunk borers detected in several countries throughout the Americas (Fawcett 1906; Costa-Lima 1956; Janzen 1987; Bravo and Zunino 1998; Gripenberg et al. 2019; Díaz-Grisales et al. 2021; Rodríguez-Sánchez et al. 2022), while records in *Annona* are known for only three trunk borers from Brazil (Ihering 1909; Costa-Lima 1956; Silva et al. 1968; Vanin and Bená 2015). The occurrence of *Heilipus* on *Annona* trunks was probably first documented by Ihering (1909) and subsequently by Costa-Lima (1956), Silva et al. (1968) and Vanin and Bená (2015), who reported the interaction of *H. gibbus* Vanin & Bená, *H. lactarius* Germar and *H. velamen* Boheman with five plant species of this genus. Regarding trunk borers associated

with the family Lauraceae, an additional host plant for *H. catagraphus* belonging to the genus *Nectandra* Rol. ex Rottb. was identified by Bondar (1915), while *H. peplus* Guérin (Fig. 1G) was reported as a trunk borer of an *Ocotea* Aubl. species in southern Brazil (Costa-Lima 1956; Silva et al. 1968). While the infestation and damage caused by the trunk and branch borers of the genus *Heilipus* have been predominantly observed in cultivated plants, the spermophagous species have been recorded in cultivated, native and endemic plants.

The available evidence indicates that the seed-boring habit of *Heilipus* is exclusive to the family Lauraceae (Vernalha 1953; Gripenberg et al. 2019; Downey et al. 2020; Díaz-Grisales et al. 2021; Pessotto et al. 2021; Rodríguez-Sánchez et al. 2022; Sanz-Veiga et al. 2024). Besides *Persea*, in South America, the genera *Nectandra* and *Ocotea* have been reported to host *H. draco* (Fabricius) (Fig. 1B), *H. odoratus* Vanin & Gaiger, *H. parvulus* Boheman and *H. vividaensis* Sanz-Veiga, Savaris & Leivas in Brazil (Vernalha 1953; Costa-Lima 1956; Hirano 2004; Vanin and Gaiger 2005; Carvalho et al. 2009; Pessotto et al. 2021; Sanz-Veiga et al. 2024) and the genus *Aniba* Aubl. for *H. longirostris* (Champion) in Colombia (Díaz-Grisales et al. 2021). In Central America, ecological studies of seed predators in tropical forests have provided valuable information on the interactions of *H. draco* with plants of the genera *Aiouea* Aubl., *Beilschmiedia* Nees., *Nectandra* and *Ocotea* in Panama (Gripenberg et al. 2019; Downey et al. 2020) and *Mespilodaphne* Nees & Mart. ex Nees. in Costa Rica (Janzen 1987). In North America, natural occurrences of seed predators of the genus *Heilipus* have only been reported in Mexico, specifically in the genera *Damburneya* Raf. and *Nectandra* (Sánchez-Garduño 1995; Rodríguez-Sánchez et al. 2022).

Much of these data was published in Brazil and the United States during the 20th century, primarily in catalogues and books on crop pests (Ihering 1909; Bondar 1915; Costa-Lima 1956; Silva et al. 1968) and in papers on avocado borers (Barber 1912, 1919; Dietz and Barber 1920; Wolfenbarger 1948, 1950; Woodruff 1963). In this century, the results of ecological (Bravo and Sallenave 2003; Bravo 2008; Gripenberg et al. 2019; Downey et al. 2020; Sánchez-Rodríguez et al. 2022), taxonomic (Vanin and Gaiger 2005; Díaz-Grisales 2019; Díaz-Grisales et al. 2021; Sanz-Veiga et al. 2024), agricultural (Lourenção et al. 2003; Castañeda-Vildózola et al. 2009, 2010; Rubio et al. 2009) and forestry studies (Hirano 2004; Spironello et al. 2004; Gómez and Toro 2007; Carvalho et al. 2009) involving Lauraceae have contributed to a greater understanding of the host plants of these weevils and have revealed that their association with this botanical family extends beyond avocado. Despite this progress, two centuries after the description of the genus by Germar (1824), the habits and host plants of only 20 species are known. Currently, information on *Heilipus* is still generally scarce, originating from a multitude of sources, including scientific papers, dissertations, catalogues, books, bulletins, agricultural reports and others. Therefore, the objective of this study was to compile and present the available knowledge on the habits and host plants of *Heilipus*, as well as to provide new information derived from the revision of specimens identified in museums and entomological collections. This review is part of a larger, ongoing project that aims to conduct a systematic revision of the genus *Heilipus*, addressing gaps in taxonomic identification and phylogenetic relationships within the group and uncovering evolutionary trends related to host plant use.

Materials and methods

The host plants recorded for *Heilipus* species were compiled, based on a bibliographic survey and collection data on labels of material examined in entomological museums and collections. A plant was considered as a host for a *Heilipus* species only if there was evidence of immature stages developing in the plant tissue (e.g. seeds or trunk and branch bark), either in literature reports or in collection data of the material examined. Records of adults collected or found on a plant species without reference to rearing on plant tissue were not included.

Revision of bibliographic resources

A systematic search for references was conducted using academic databases with a range of key terms, including “Annonaceae borers”, “avocado weevils”, “*Heilipus*”, “*Heilipus* Annonaceae”, “*Heilipus* host plants”, “*Heilipus* Lauraceae”, “Lauraceae borers”, “Lauraceae seed predators” and “Lauraceae trunk borers”, amongst others. Additionally, references cited in agricultural reports, books, bulletins, catalogues, checklists, dissertations and scientific papers on the genus *Heilipus* published since approximately 1900 were tracked.

The main objective of this study is to provide a summary of the host plant-*Heilipus* species associations known to date, not to list all the instances where a given association has been reported in the literature or found in entomological collections. Therefore, each association is presented once per country, using the bibliographic reference where it was first mentioned. In many cases, the document mentioning an interaction for the first time is the only one available, but in the case of economically important plant genera such as *Annona* or *Persea*, there are many more reports. In some of these cases, more than one reference per country was provided to clarify the host plant variety or cultivar involved in the interaction or to improve the distribution records at least at the state/province or municipality level.

Occurrence information extracted from the bibliographic resources used (e.g. locality and coordinates when available) can be consulted through the link provided in the Data resources section.

Material examined

A total of 931 specimens of the genus *Heilipus* were examined in 20 natural history collections in Brazil (20 specimens), Colombia (249), Mexico (142), United Kingdom (118) and United States (402). These collections are listed below:

CEAH	Coleção Entomológica Adolph Hempel, Instituto Biológico, São Paulo, Brazil.
CEAM	Colección Entomológica del Colegio de Postgraduados, Campus Montecillo, State of Mexico, Mexico.
CEBAJ-INIFAP	Colección Nacional de Insectos del Campo Experimental Bajío del INIFAP, Centro de Investigación Regional Centro, Guanajuato, Mexico.
CEUA	Colección de Entomología de la Universidad de Antioquia, Antioquia, Colombia.
CEUNP	Colección de Entomología de la Universidad Nacional Sede Palmira, Valle del Cauca, Colombia.
CNIN	Colección Nacional de Insectos del Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico.
CNRF-DGSV	Colección de Entomología y Acarología del Centro Nacional de Referencia Fitosanitaria, Dirección General de Sanidad Vegetal - SENASICA, State of Mexico, Mexico.
CTNI	Colección Taxonómica Nacional Luis María Murillo, Centro de Investigación Tibaitatá de AGROSAVIA, Cundinamarca, Colombia.
IAvH-E	Colección de Entomología del Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Boyacá, Colombia.
ICN	Colección de Coleoptera del Instituto de Ciencias Naturales, Universidad Nacional Sede Bogotá, Bogotá, D. C., Colombia.
IEXA	Colección Entomológica del Instituto de Ecología, A.C., Veracruz, Mexico.
LEUC	Colección del Laboratorio de Entomología de la Universidad de Caldas, Caldas, Colombia.
MEFLG	Museo Entomológico Francisco Luis Gallego, Universidad Nacional Sede Medellín, Antioquia, Colombia.
MEMB	Museo Entomológico Marcial Benavides, Cenicafé, Caldas, Colombia.
MPUJ_ENT	Colección Entomológica del Museo Javeriano de Historia Natural, Pontificia Universidad Javeriana, Bogotá, D. C., Colombia.
MUSENUV	Museo de Entomología de la Universidad del Valle, Valle del Cauca, Colombia.
MZFC	Museo de Zoología Alfonso L. Herrera, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, Mexico.
NHMUK	Natural History Museum, London, England, United Kingdom.
UNAB	Museo Entomológico de la Facultad de Ciencias Agrarias, Universidad Nacional Sede Bogotá, Bogotá, D. C., Colombia.
USNM	Smithsonian National Museum of Natural History, Department of Entomology, Washington, D.C., United States of America.

Only 40% of the examined specimens had information on their habits and host plants. Furthermore, only 7% of these 40% corresponded to plants other than avocado. Consequently, occurrence data from only 85 specimens are presented (Data resources section), providing information on 12 host plant associations not previously reported in the literature. These 85 specimens belong to 13 locality records for 10 *Heilipus* species and are deposited at the CEAH, MEFLG and USNM.

Botanical names

All botanical names and plant synonyms used correspond to the names and taxonomic treatment accepted in The Word Flora Online (WFO 2024) at the time of access.

Data resources

The data underpinning the analysis reported in this paper are deposited in the Dryad Data Repository at https://doi.org/10.5061/dryad.0cfxpnwbn.

Results

Habits and biology

Seed predators
(Fig. 1A–D)

The biology of spermophagous species begins with the female boring into the fruit to deposit her eggs as close to the seed as possible. This oviposition occurs in fruits that are attached to the tree (Downey et al. 2020; Rodríguez-Sánchez et al. 2022), placing this genus in the category of pre-dispersal seed predators. In small fruits, such as those of the genera *Aniba* Aubl. or *Ocotea* Aubl. (Lauraceae), oviposition is common towards the final

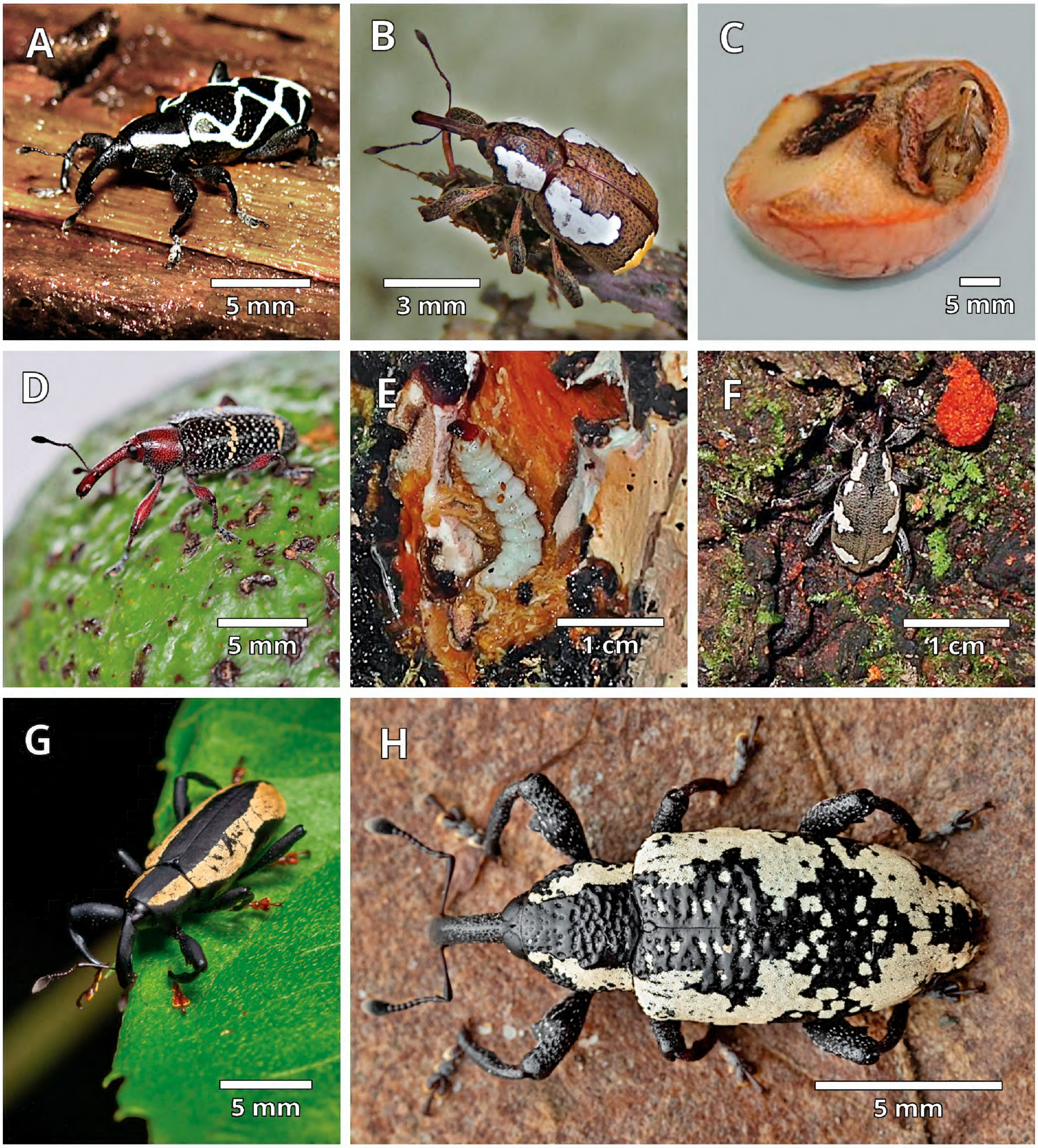

Figure 1. Some species of the genus *Heilipus*: **A.** *Heilipus albovenosus* (Champion), seed borer; **B.** *Heilipus draco* (Fabricius), seed borer; **C.** Pupa of *Heilipus lauri* Boheman inside an avocado seed; **D.** Adult of *H. lauri* perching on an avocado fruit; **E.** Larva of *Heilipus albopictus* (Champion) inside an avocado trunk; **F.** Adult of *H. albopictus* at the base of an avocado tree trunk; **G.** *Heilipus peplus* Guérin, trunk borer; **H.** *Heilipus squamosus* (LeConte), trunk borer. Credits: **A.** Courtesy of Robby Deans, iNaturalist user (@hydaticus); photograph available at https://www.inaturalist.org/observations/486181; **B.** Courtesy of Diogo Luiz, iNaturalist user (@diogoluiz); photograph available at https://www.inaturalist.org/observations/31955954; **C, D.** Díaz-Grisales et al. (2017); **E, F.** Castañeda-Vildózola et al. (2010); **G.** Courtesy of Bernardo Rodrigues Ferraz, iNaturalist user (@bernardofrz); photograph available at https://www.inaturalist.org/observations/112606521; **H.** Courtesy of Ken Bluma, iNaturalist user (@kbmacroart); photograph available at https://www.inaturalist.org/observations/240090778.

development of the fruit (Spironello et al. 2004), ripe or unripe (Vernalha 1953; Pessotto et al. 2021). In larger fruits, such as avocado, oviposition also occurs while the fruit is attached to the tree, but often during growth; for example, a high incidence of damage by *H. lauri* (Fig. 1D) was observed when avocado fruits reached 4 to 5 cm in diameter (Castañeda-Vildózola et al. 2017) or a length between 3 and 12 cm (Caicedo et al. 2010).

Fruits with small oviposition punctures (Bravo 2008), perforations or holes in the epidermis with the presence of a black or dark circular scab (Caicedo et al. 2010) are signs of the infestation by species of the genus *Heilipus*. From one to three eggs per fruit have been reported in avocado fruits attacked by *H. lauri* (Castañeda-Vildózola et al. 2013) and *H. trifasciatus* (Santos-Murgas et al. 2014). Pessotto et al. (2021) also reported one to three eggs per fruit in *Ocotea puberula* (Rich.) Nees fruits infested by *H. draco*, with one egg per fruit being the most common finding. In avocado fruits, whitish exudates around the perforations are indicatives of infestation by these weevils (Castañeda-Vildózola et al. 2013).

The emerging larva feeds on the endosperm, where it completes all its larval development. Larvae are cannibalistic and this behaviour usually results in only one larva per seed (Castañeda-Vildózola et al. 2017; Pessotto et al. 2021; Rodríguez-Sánchez et al. 2022). However, it is possible to find two or up to four larvae in large seeds, such as those of avocado (Dietz and Barber 1920; Santos-Murgas et al. 2014; Castañeda-Vildózola et al. 2017). Although larval development inside the seed often causes abortion or premature drop of the infested fruit (Peña 1998), in some cases, the fruit remains attached to the tree even when the pupa or adult is fully developed (Castañeda-Vildózola et al. 2009). The pupal stage also occurs inside the seed (Fig. 1C). Upon completion of metamorphosis, the adult makes a hole with its mandibles to emerge from the seed (Vanin and Gaiger 2005; Santos-Murgas et al. 2014; Díaz-Grisales et al. 2017). This frequently occurs when the fruit has fallen to the ground (Vernalha 1953; Pessotto et al. 2021). Adult feeding targets in spermophagous and trunk-boring species, include leaves, buds, tender shoots, young branches and growing fruits without affecting the seeds. Damage to these structures is considered secondary and of no economic importance (Wolfenbarger 1948; Lourenção et al. 1984; Castañeda-Vildózola et al. 2010; Díaz-Grisales et al. 2017).

Damage rates, at least for the species for which this has been documented, are highly variable. Reported incidences range from 0.06% of *O. puberula* fruits infested by *H. draco* (Fig. 1B) in Panama (Downey et al. 2020), 16% of *Damburneya ambigens* (S.F. Blake) Trofimov seeds damaged by *H. albomaculatus* (Champion) in Mexico (Rodríguez-Sánchez et al. 2022), 42.5% of wild avocado seeds injured by larvae of *H. trifasciatus* in Panama (Dietz and Barber 1920), 75% of *Aniba rosodora* Ducke fruits attacked by *H. odoratus* in Brazil (Morais et al. 2009) and up to 80% of avocado fruits infested by *H. lauri* in backyard orchards in Mexico (Castañeda-Vildózola et al. 2013). Infestation by spermophagous species of *Heilipus* can affect seed germination because the larvae consume the embryo and its reserves, leaving only the seed integument (Gómez and Toro 2007; Pessotto et al. 2021). However, seeds can germinate if the embryo is not damaged (Barber 1919; Spironello et al. 2004; Bravo 2008).

Trunk borers
(Fig. 1E–H)

The habits and biology of the trunk borers of the genus *Heilipus* are known primarily from the species that attack avocado in the Americas. Similar habits and behaviour, although poorly documented, have been observed in the species that bore into the trunks of the family Annonaceae. The female lays eggs in the bark, usually at the base of the tree, in the root collar area (Wolfenbarger 1948; Lourenção et al. 2003). Oviposition is most common at the base of the tree, but can also occur in the lower branches and thick roots near or below the ground (Lourenção et al. 2003; Moura et al. 2006; Rubio et al. 2009). In avocado, oviposition and damage caused by *Heilipus* species have been documented on trees ranging from 0.5 years old (Wolfenbarger 1948) and up to more than 30 years old (Rubio et al. 2009). In Florida orchards (USA), most signs of infestation by *H. squamosus* (Fig. 1H) larvae were observed in the first 15.24 cm (6 inches) above the ground in small avocado trees with a diameter of 7.62–15.24 cm (3–6 inches) (Wolfenbarger 1948). In the State of Mexico (Mexico), oviposition by *H. albopictus* (Fig. 1F) was recorded 40 cm above the ground in stems of Mexican criollo avocado (Castañeda-Vildózola et al. 2010). In the Department of Tolima (Colombia), the incidence of *H. elegans* larvae was higher at the base of common or criollo avocado trees that were older than 30 years and exceeded 15 m in height (Rubio et al. 2009). Signs of infestation by these borers are reddish-orange masses of faeces and exudates on the trunk caused by larval feeding, usually near or at ground level, in the shaded areas of the trunk and branches (Wolfenbarger 1948; Rubio et al. 2009; Castañeda-Vildózola et al. 2010). The masses tend to crumble and be washed away by rain (Wolfenbarger 1948).

After emerging from the egg, the larvae begin to feed on the subcortical tissues (Fig. 1E), between the bark and the vascular cambium layer, leaving a gallery as they feed, plugging or blocking the gallery with their excrement (Lourenção et al. 2003; Wolfenbarger 1948). From one (Wolfenbarger 1948) to up to 30 larvae (Rubio et al. 2009) have been found in a single avocado trunk infested with borers of the genus *Heilipus*. Once larval development is complete, pupation occurs in a cell previously built by the larva between the bark and the wood of the tree (Castañeda-Vildózola et al. 2010). Finally, the adult emerges from the trunk. Losses and incidence rates reported vary from 8% to 10% of the trees in an avocado orchard infested by *H. squamosus* in Florida, USA (Wolfenbarger 1948); 30% of avocado trees killed by feeding of *H. rufipes* larvae in Ceará, Brazil (Lourenção et al. 2003); and 49.1% of avocado trunks infested by *H. elegans* larvae in orchards from Tolima, Colombia (Rubio et al. 2009). In contrast, there are no records of the incidence, percentage of damage or number of larvae found in trunks for the species that attack plants in the family Annonaceae. Symptoms of infestation by trunk borers of the genus *Heilipus* include yellowing of leaves, defoliation, drying

of branches, girdling, wilting and even death of affected trees (Wolfenbarger 1948; Lourenção et al. 1984, 2003; Rubio et al. 2009; Castañeda-Vildózola et al. 2013).

Plant genera with occurrence of *Heilipus* species

Species in the genus *Heilipus* are associated with at least 13 plant genera belonging to the families Annonaceae (one genus) and Lauraceae (12 genera). These associations are summarised in Table 1 and described in detail below.

Aiouea Aubl. (Lauraceae)

In Barro Colorado Island, Panama, Gripenberg et al. (2019) recorded the emergence of adults of *H. draco* from seeds of *Cinnamomum triplinerve*, one of the synonyms of the species *Aiouea montana* (Se.) R. Rohde.

Aniba Aubl. (Lauraceae)

Larvae of *H. odoratus* feeding on seeds of *A. rosodora* Ducke in Manaus, Amazonas State, Brazil (Vanin and Gaiger 2005). In Colombia, Gómez and Toro (2007) reported that an unidentified species of the genus *Heilipus* attacks the seeds of *Aniba perutilis* Hemsl. in Andean forests. In addition, four specimens of *H. longirostris* (Díaz-Grisales et al. 2021) and two of a verified new *Heilipus* species (*Heilipus* sp. nov. VDG6) were obtained from seeds of *Aniba* sp. collected in San Francisco, Department of Antioquia. The two specimens of *Heilipus* sp. nov. VDG6 are deposited at the MEFLG. With 20 species, *Aniba* is one of the five richest genera of Lauraceae in Colombia (Raz and Agudelo Zamora 2023).

Annona L. (Annonaceae)

The association of *Heilipus* species with this genus and this family has been reported only in trunks and only in states of the south and southeast regions of Brazil. *Heilipus gibbus* has been recorded damaging the trunks of soursop (*A. muricata* L.) and the hybrid atemóia (*A. cherimola* Mill. × *A. squamosa* L.) in the States of Distrito Federal and São Paulo (Vanin and Bená 2015). *Heilipus lactarius* on trunks of biribá (*A. mucosa* Jacq.), fruta-do-conde (*A. reticulata* L.) and araticum-do-mato (*A. sylvatica* A. St.-Hil.) in Minas Gerais, Rio de Janeiro and São Paulo (Costa-Lima 1956; Silva et al. 1968). *Heilipus velamen* has been found in trunks of *A. reticulata* in the States of Espírito Santo, Rio de Janeiro and São Paulo (Costa-Lima 1956; Silva et al. 1968). There are also reports of *H. catagraphus* damaging the base of the trunks of *A. mucosa* (Silva et al. 1968), *A. muricata* (Moura et al. 2006; Braga Sobrinho et al. 2011) and *A. reticulata* (Ihering 1909) in Brazil. However, these records may be the result of erroneous identifications, as *H. gibbus* was frequently misidentified as *H. catagraphus* (Vanin and Bená 2015). According to Vanin and Bená (2015), it is possible that *H. gibbus* is exclusively associated with plant trunks of the family Annonaceae, while *H. catagraphus* is associated with the trunks of the family Lauraceae.

Annona mucosa is native to the southeast and other regions of Brazil (Flora e Funga do Brasil 2024), whereas *A. reticulata* is cultivated in several States, including Minas Gerais, Rio de Janeiro and São Paulo (Flora e Funga do Brasil 2024). *Annona sylvatica*, an endemic species to Brazil, is less widely distributed than *A. mucosa*, but is also present in the southeast and other regions of the country (Flora e Funga do Brasil 2024).

Beilschmiedia Nees. (Lauraceae)

In Barro Colorado Island, Panama, 116 individuals of *H. draco* emerged from 3404 fruits of *B. tovarensis* (Klotzsch & H. Karst. ex Meisn.) Sach. Nishida collected by Downey et al. (2020) over a period of two years.

Caryodaphnopsis Airy Shaw. (Lauraceae)

Two additional adults of *Heilipus* sp. nov. VDG6 were found at the MEFLG. Based on the associated label data, these individuals emerged from seeds of *C. cogolloi* van der Werff, a species endemic to Colombia, collected in the Municipality of San Luis, Antioquia. Seven species of *Caryodaphnopsis* are found in Colombia, three of which are endemic (Mendoza-Cifuentes et al. 2023). The distribution of *C. cogolloi* is limited to the Reserva Natural Cañón del Río Claro El Refugio in the Department of Antioquia, where it is critically endangered due to timber overexploitation (Polanco et al. 2014).

Cinnamomum Schaeff. (Lauraceae)

Examination of the material deposited at the USNM yielded ten specimens of *H. draco*, which, according to their labels, emerged from seeds of the cinnamon tree (*C. verum* J. Presl) from Trinidad and Tobago. Similarly, 20 adults of the same species were found at the CEAH, which emerged from seeds of *C. verum* collected in the Municipality of Campinas, São Paulo State, Brazil. For *H. draco*, these two findings represent a new host plant record. *Heilipus mirus* is another species associated with the genus *Cinnamomum*. It causes damage to the bark of camphor trees (*C. camphora* (L.) J. Presl) in Jamaica. The association between *H. mirus* and *C. camphora* rectifies an error that arose more than a century ago. In 1905, William Fawcett, the director of Jamaica's Public Gardens and Plantations, sent Leland Ossian Howard, then chief of the Bureau of Entomology of the United States Department of Agriculture, samples of an insect that was attacking young camphor trees at the Cinchona Botanical Garden in Jamaica. Regarding the samples, Howard informed Fawcett that "…Mr. Schwarz [probably referring to the entomologist Eugene Amandus Schwarz] reports that the weevil is *Hilipus* [sic] *elegans*, Guérin of the family Curculionidae." Fawcett (1906) published this

Table 1. Summary of the host plants of the genus *Heilipus* Germar in ten countries of the Americas. [1] According to Rohwer (2000), Chanderbali et al. (2001), Rohwer and Rudolph (2005) and Song et al. (2017). Identifications obtained from bibliographic sources are presented in the same form as they appear in the cited references (e.g. *Heilipus* sp. or *Heilipus* sp. cur15SG). The identifiers with letters VDG correspond to codes assigned to new species that will be described in the ongoing taxonomic revision of the genus *Heilipus*. Abbreviations: S = seed borer, T = trunk borer, N/A = not applicable.

***Heilipus* species**	**Habit**	**Plant species**	**Botanical family**	**Lineage within family Lauraceae[1]**	**Country where the association was recorded**	**Bibliographic reference or entomological collection**
H. albomaculatus	S	*Damburneya ambigens*	Lauraceae	Cinnamomeae	Mexico	Rodríguez-Sánchez et al. (2022)
		Damburneya gentlei				
H. albovenosus	S	*Damburneya coriacea*	Lauraceae	Cinnamomeae	Mexico	USNM
H. draco	S	*Aiouea montana*	Lauraceae	Cinnamomeae	Panama	Gripenberg et al. (2019)
		Beilschmiedia tovarensis	Lauraceae	*Cryptocarya* group - *Beilschmiedia* complex	Panama	Downey et al. (2020)
		Cinnamomum verum	Lauraceae	Cinnamomeae	Brazil	CEAH
					Trinidad and Tobago	USNM
		Damburneya salicifolia	Lauraceae		Mexico	Rodríguez-Sánchez et al. (2022)
		Mespilodaphne veraguensis	Lauraceae		Costa Rica	Janzen (1987)
		Nectandra angustifolia	Lauraceae		Brazil	Sanz-Veiga et al. (2024)
		Nectandra cissiflora	Lauraceae		Panama	Gripenberg et al. (2019)
		Nectandra lineata				Downey et al. (2020)
		Ocotea leptobotra	Lauraceae		Panama	Downey et al. (2020)
		Ocotea oblonga				
		Ocotea porosa			Brazil	Hirano (2004)
		Ocotea puberula			Brazil	Pessotto et al. (2021)
					Panama	Downey et al. (2020)
H. empiricus	S	*Ocotea glaucosericea*	Lauraceae	Cinnamomeae	Costa Rica	USNM
H. guttiger	S	*Damburneya salicifolia*	Lauraceae	Cinnamomeae	Mexico	Rodríguez-Sánchez et al. (2022)
		Damburneya salicina			Costa Rica	USNM
		Nectandra turbacensis			Mexico	Rodríguez-Sánchez et al. (2022)
Heilipus aff. *hopei*	S	*Clinostemon mahuba*	Lauraceae	*Mezilaurus* group	Brazil	Costa-Lima (1956)
H. lauri	S	*Persea americana*	Lauraceae	*Persea* group	Colombia	Gallego (1949)
					Mexico	Schoenherr (1845), Barber (1919)
		Persea schiedeana			Mexico	Castañeda-Vildózola et al. (2009)
H. longirostris	S	*Aniba* sp.	Lauraceae	Cinnamomeae	Colombia	Díaz-Grisales et al. (2021)
		Mezilaurus sp.		*Mezilaurus* group		MEFLG
H. odoratus	S	*Aniba rosodora*	Lauraceae	Cinnamomeae	Brazil	Vanin and Gaiger (2005)
H. parvulus	S	*Ocotea porosa*	Lauraceae	Cinnamomeae	Brazil	Vernalha (1953)
H. pittieri	S	*Persea americana*	Lauraceae	*Persea* group	Costa Rica	González-Herrera (2003)
					Nicaragua	Maes (2004)
		Persea schiedeana			Costa Rica	Barber (1919)
Heilipus sp. nov. VDG1	S	*Damburneya salicina*	Lauraceae	Cinnamomeae	Costa Rica	USNM
		Ocotea floribunda				
Heilipus sp. nov. VDG6	S	*Aniba* sp.	Lauraceae	Cinnamomeae	Colombia	MEFLG
		Caryodaphnopsis cogolloi		*Caryodaphnopsis*		
Heilipus sp.	S	*Aniba perutilis*	Lauraceae	Cinnamomeae	Colombia	Gómez and Toro (2007)
Heilipus sp.	S	*Nectandra nitidula*	Lauraceae	Cinnamomeae	Brazil	Carvalho et al. (2009)
Heilipus sp.	S	*Ocotea diospyrifolia*	Lauraceae	Cinnamomeae	Argentina (Brasilera Island)	Bravo and Sallenave (2003)
Heilipus sp.	S	*Ocotea puberula*	Lauraceae	Cinnamomeae	Argentina (Brasilera Island)	Bravo and Zunino (1998)
Heilipus sp. cur15SG	S	*Ocotea whitei*	Lauraceae	Cinnamomeae	Panama	Gripenberg et al. (2019)
H. trifasciatus	S	*Persea americana*	Lauraceae	*Persea* group	Colombia	Díaz-Grisales et al. (2020)
					Costa Rica	González-Herrera (2003)
					Panama	Dietz and Barber (1920), Santos-Murgas et al. (2014)
		Persea spp.			Nicaragua	Maes and O'Brien (1990)

Heilipus species	Habit	Plant species	Botanical family	Lineage within family Lauraceae[1]	Country where the association was recorded	Bibliographic reference or entomological collection
H. vividaensis	S	*Nectandra angustifolia* *Ocotea puberula*	Lauraceae	Cinnamomeae	Brazil	Sanz-Veiga et al. (2024)
H. albopictus	T	*Persea americana*	Lauraceae	*Persea* group	Mexico	Castañeda-Vildózola et al. (2010)
H. catagraphus	T	*Nectandra venulosa* *Persea americana*	Lauraceae	Cinnamomeae *Persea* group	Brazil	Bondar (1915), Costa-Lima (1956), Silva et al. (1968)
H. elegans	T	*Persea americana*	Lauraceae	*Persea* group	Colombia Costa Rica	Rubio et al. (2009) González-Herrera (2003)
H. fassli	T	*Persea americana*	Lauraceae	*Persea* group	Colombia	MEFLG
H. gibbus	T	*Annona cherimola* Mill. × *Annona squamosa* L. *Annona muricata*	Annonaceae	N/A	Brazil	Vanin and Bená (2015)
H. lactarius	T	*Annona mucosa* *Annona reticulata* *Annona sylvatica*	Annonaceae	N/A	Brazil	Silva et al. (1968) Costa-Lima (1956) Silva et al. (1968)
H. leopardus	T	*Persea americana*	Lauraceae	*Persea* group	Colombia	Díaz-Grisales (2019)
H. mirus	T	*Cinnamomum camphora*	Lauraceae	Cinnamomeae	Jamaica	USNM
H. peplus	T	*Ocotea catharinensis*	Lauraceae	Cinnamomeae	Brazil	Costa-Lima (1956), Silva et al. (1968)
H. rufipes	T	*Persea americana*	Lauraceae	*Persea* group	Brazil	Lourenção et al. (2003)
H. squamosus	T	*Persea americana* *Damburneya coriacea*	Lauraceae	*Persea* group Cinnamomeae	United States	Wolfenbarger (1948) USNM
H. velamen	T	*Annona reticulata*	Annonaceae	N/A	Brazil	Costa-Lima (1956), Silva et al. (1968)

information in the Bulletin of the Jamaica Department of Agriculture. Since then, it is believed that *H. elegans*, a species known to bore avocado trunks in Colombia (Rubio et al. 2009, see below), can also cause damage to *C. camphora*. However, one of the specimens received by Howard was physically examined at the USNM by the first author of this work and it was discovered that it did not belong to the species *H. elegans*, but to *H. mirus*. Therefore, the only confirmed host plant so far for *H. elegans* is *P. americana*, while the association of *H. mirus* with *C. camphora* represents a new report of habit and host plant for this *Heilipus* species.

Clinostemon Kuhlm. & A. Samp. (Lauraceae)

A species close to *H. hopei* Boheman was obtained by Costa-Lima (1956) from a seed of *Licaria mahuba* from Pará, Brazil. Currently, *L. mahuba* is considered a synonym of *Clinostemon mahuba* (A. Samp.) Kuhlm. & Samp. (Flora e Funga do Brasil 2024).

Damburneya Raf. (Lauraceae)

Three spermophagous species of *Heilipus* have been recorded in this genus of plants in the tropical rainforest of Los Tuxtlas Biosphere Reserve, situated within the Mexican State of Veracruz: *H. albomaculatus* in seeds of *D. ambigens* (S.F. Blake) Trofimov and *D. gentlei* (Lundell) Trofimov and *H. draco* and *H. guttiger* (Champion) in seeds of *D. salicifolia* (Kunth) Trofimov & Rohwer (Rodríguez-Sánchez et al. 2022). Additionally, from Mexico, the USNM houses a specimen of *H. albovenosus* (Champion) (Fig. 1A) obtained from a fruit of *D. coriacea* (Sw.) Trofimov & Rohwer from the Municipality of Tampico, State of Tamaulipas. The native range of *D. coriacea* extends from Mexico to Central America and from southern Florida to the Caribbean (WFO 2024). This is the first time that the habit and host plant of *H. albovenosus* have been reported.

In Costa Rica, five adults of a verified new species of *Heilipus* (*Heilipus* sp. nov. VDG1) and one of *H. guttiger* emerged from seeds of *D. salicina* (C.K. Allen) Trofimov & Rohwer collected in Monteverde, Puntarenas Province. In addition, a specimen of the trunk borer *H. squamosus* was found in wood of *D. coriacea* in the locality of Noble, Georgia, United States. The reports of *H. guttiger* in *D. salicina* and *H. squamosus* in *D. coriacea* represent new host plant records for these *Heilipus* species; both specimens, along with the five *Heilipus* sp. nov. VDG1, are deposited at the USNM.

Mespilodaphne Nees & Mart. ex Nees. (Lauraceae)

In Santa Rosa National Park, Guanacaste Province, Costa Rica, *H. draco* is a seed predator of *M. veraguensis* (Meisn.) Rohwer (Janzen 1987).

Mezilaurus Kuntze ex Taub. (Lauraceae)

Five adults of *H. longirostris* were obtained from seeds of an unidentified species of *Mezilaurus* collected in the Municipality of San Luis, Department of Antioquia, Colombia; these specimens are deposited at the MEFLG. This finding represents a new host plant genus record for *H. longirostris*. Notably, the genus *Mezilaurus* has only four recorded species in Colombia (Raz and Agudelo Zamora 2023).

Nectandra Rol. ex Rottb. (Lauraceae)

Within this genus, *Heilipus* species have been reported in both seeds and trunks. Two adults of *H. guttiger* emerged from seeds of *N. turbacensis* (Kunth) Nees collected in the rainforest of Los Tuxtlas, Veracruz, Mexico (Rodríguez-Sánchez et al. 2022). In Barro Colorado Island, Panama, *H. draco* has been recorded on seeds of *N. cissiflora* Nees (Gripenberg et al. 2019; Downey et al. 2020) and *N. lineata* (Kunth) Rohwer (Downey et al. 2020). In Brazil, Sanz-Veiga et al. (2024) obtained adults of *H. draco* and *H. vividaensis* from seeds of *N. angustifolia* (Schrad.) Nees & Mart. collected in the Municipality of Guapiara, State of São Paulo. They also recorded the occurrence of *H. draco* in seeds of *N. angustifolia* from Piracicaba, also in São Paulo State (Sanz-Veiga et al. 2024). In the State of Minas Gerais, Carvalho et al. (2009) reported an undetermined species of the genus *Heilipus* as a seed predator of *N. nitidula* Nees & Mart. in the Municipality of Poços de Caldas. Finally, *H. catagraphus* has been documented as a trunk borer of *N. venulosa* Meisn., commonly known as canelinha, in Brazil (Bondar 1915; Costa-Lima 1956; Silva et al. 1968). *Nectandra venulosa* is endemic to Brazil, only having been recorded from the State of Minas Gerais (Flora e Funga do Brasil 2024).

Ocotea Aubl. (Lauraceae)

Amongst the genera of Lauraceae, *Ocotea* has the largest number of records of spermophagous species of *Heilipus*, especially *H. draco* (Fig. 1B) and other morphologically similar species. In Monteverde, Puntarenas Province, Costa Rica, one adult of *H. empiricus* (Pascoe) was obtained from a seed of *O. glaucosericea* Rohwer and six other adults of *Heilipus* sp. nov. VDG1 from seeds of *O. floribunda* (Sw.) Mez; these seven specimens are deposited at the USNM. The occurrence of *H. empiricus* in *O. glaucosericea* seeds is a new record of the habit and host plant of this species of *Heilipus*. In Barro Colorado Island, Panama, Gripenberg et al. (2019) obtained an adult of an undetermined *Heilipus* species (*Heilipus* sp. cur15SG) from seeds of *O. whitei* Woodson. In the same locality, Downey et al. (2020) recorded the emergence of *H. draco* specimens from seeds of *O. leptobotra* (Ruiz & Pav.) Mez, *O. oblonga* (Meisn.) Mez and *O. puberula* (Rich.) Nees.

In Brazil, *H. draco* adults have also been obtained from *O. puberula* seeds collected in the Municipality of Taquaruçu do Sul, Rio Grande do Sul (Pessotto et al. 2021) and from *O. porosa* (Nees & Mart.) Barroso seeds collected in the Canoinhas Region, State of Santa Catarina (Hirano 2004). *Heilipus parvulus* is another species that has been documented as a seed predator of *O. porosa* in Ponta Grossa, Paraná (Vernalha 1953). Additionally, in the State of Paraná, Sanz-Veiga et al. (2024) obtained adults of *H. vividaensis* from fruits of *O. puberula* collected in the Municipality of Coronel Vivida. In Argentina, seeds of *O. diospyrifolia* (Meisn.) Mez (Bravo and Sallenave 2003) and *O. puberula* (Bravo and Zunino 1998) infested with larvae of an undetermined species of *Heilipus* were collected in Brasilera Island, an area located at the confluence of the Paraná and Paraguay Rivers. Finally, only one species has been reported in the trunks of *Ocotea*. According to Costa-Lima (1956) and Silva et al. (1968), the larvae of *H. peplus* (Fig. 1G) bore canela-preta (*O. catharinensis* Mez) in Rio Grande do Sul, Brazil.

Persea Mill. (Lauraceae)

This is the plant genus from which *Heilipus* has traditionally been recorded, mainly because of the damage that some of its species cause to the seeds and trunks of avocado (*P. americana*), one of the most economically important species of the family Lauraceae.

Seed predators of the genus *Persea* include the species *H. lauri* (Fig. 1C, D), *H. pittieri* and *H. trifasciatus*. Another species documented on avocado seeds is *Heilipus montei* Costa-Lima, a synonym of *H. parvulus* according to Kuschel (1958). *Heilipus montei* was described, based on four specimens that were purportedly obtained from avocado fruits collected in Conceição do Serro, Minas Gerais State, Brazil (Costa-Lima 1935). Nevertheless, this association is suspect as it has not been corroborated or found again since the description of *H. montei* by Costa-Lima in 1935.

In Mexico, larvae and adults of *H. lauri* have been found in seeds of commercial cultivars and varieties of *P. americana* (Schoenherr 1845; Barber 1919) in the States of Chiapas, Guerrero, Hidalgo, Mexico, Morelos, Oaxaca, Puebla and Veracruz (Castañeda-Vildózola et al. 2013; Vázquez et al. 2017). Amongst the commercial cultivars are Choquette, Colín V-33, Fuerte and Hass (Salgado and Bautista 1993; Medina-Quiroz et al. 2010). The avocado varieties include criollo or Mexican avocados (*P. americana* var. *drymifolia* (Schltdl. and Cham.) S.F. Blake) (Castañeda-Vildózola et al. 2017) and pahuas (*P. americana* var. *americana*) (Palacios-Torres et al. 2016). Furthermore, Castañeda-Vildózola et al. (2009) obtained *H. lauri* adults from seeds of the species *P. schiedeana* Nees collected in the Municipality of Huatusco, State of Veracruz, Mexico. In Colombia, *H. lauri* has been recorded in the fruits of *P. americana* (Gallego 1949) from the cultivars Hass (Caicedo et al. 2010) and Trinidad (Cárdenas 1984a) in the Departments of Antioquia, Caldas, Cauca, Cundinamarca, Quindío, Risaralda, Tolima and Valle del Cauca (Gallego 1949; Díaz-Grisales et al. 2017). In addition, Cárdenas (1984b) pointed out that, in the Viejo Caldas (former Colombian Department that existed between 1905 and 1966 and was comprised of the current Departments of Caldas, Quindío and Risaralda; López-Pacheco (2011)), *H. lauri* populations were more numerous and aggressive in native avocados, where trees with all fruit damaged were detected. Possibly, the native avocados mentioned by Cárdenas (1984b) may have been related to the West Indian race (*P. americana* var. *americana*), as criollo or native Colombian avocados are typical of this variety of *P. americana* (Bernal and Díaz 2020).

Like *H. lauri*, *H. pittieri* also feeds on seeds of *P. americana* (González-Herrera 2003) and *P. schiedeana* (Barber 1919) in its larval stage. Barber (1919) obtained four adults of *H. pittieri* from seeds of *Persea pittieri* Mez (one of the synonyms of *P. schiedeana*) from San José, Costa Rica; these adults are deposited at the USNM and represent the holotype, allotype and two paratypes of *H. pittieri*. Castañeda-Vildózola et al. (2013) mentioned damage by *H. pittieri* to the fruits of *P. americana* cv. Hass in Costa Rica; however, the authors did not provide the precise location of the finding. Similarly, Maes (2004) reported the occurrence of *H. pittieri* on avocado trees in Atlantic Nicaragua, yet he did not specify the cultivar or variety of avocado on which the observation was made.

Conversely, larvae and adults of *H. trifasciatus* have only been found in fruits of *P. americana* (Dietz and Barber 1920). In Colombia, the occurrence of this species attacking avocado seeds has been reported in the Municipalities of Acandí (Chocó), Palmira (Valle del Cauca) and Mistrató (Risaralda) (Díaz-Grisales et al. 2020). The report from Acandí is the only one that mentions two adults of the species emerging from seeds of native or criollo avocado (*P. americana* var. *americana*) (Díaz-Grisales et al. 2020). The avocado variety or cultivar from which the specimens were collected was not specified in the case of the Municipalities of Palmira and Mistrató. In Panama, Dietz and Barber (1920) found wild avocado seeds infested with *H. trifasciatus* larvae in Frijoles, Canal Zone. Santos-Murgas et al. (2014) reported damage by *H. trifasciatus* larvae in common or criollos avocado seeds from the community of Altos del María, Sorá, Panama. As in the case of Colombia, it is likely that the wild and criollo avocado trees mentioned by Dietz and Barber (1920) and Santos-Murgas et al. (2014) belong to or are close to the West Indian race (*P. americana* var. *americana*). González-Herrera (2003) reported that *H. trifasciatus* damages avocado fruits in Costa Rica, but he did not specify the variety or cultivar, nor the location where the observations were made. Finally, Maes and O'Brien (1990) reported the presence of *H. trifasciatus* in the Departments of Carazo, Chontales and Masaya (Nicaragua) and mentioned that it is a phytophagous species recorded on the genus *Persea*; however, they did not indicate with which species of *Persea* it is associated in that country.

To date, seven species of trunk boring *Heilipus* cause damage to the trunks and branches of varieties and commercial cultivars of *P. americana*. In the State of Florida, United States, Wolfenbarger (1948) found larvae of *H. squamosus* boring into the bark at the base of avocado trees, as well as adults feeding on fruits without affecting the seeds; however, the author did not specify the avocado variety or cultivar on which he made the observations. *Heilipus squamosus* (Fig. 1H), the sole species of *Heilipus* present in the United States, was long misidentified as *H. apiatus* (Olivier). Its presence is currently documented in 15 States across the south-eastern, south-western and mid-western regions of the country, though only in Florida has it been reported causing damage to avocado trees (Anzaldo and Díaz-Grisales 2022). In Mexico, *H. albopictus* larvae (Fig. 1E) were found in the stems of *P. americana* var. *drymifolia* in Ixtapan de la Sal and in Hass and Fuerte avocados in Coatepec Harinas, State of Mexico; damage in Hass and Fuerte cultivars was limited to the rootstock of Mexican criollo avocado (*P. americana* var. *drymifolia*) (Castañeda-Vildózola et al. 2010). In Costa Rica, González-Herrera (2003) reported *H. elegans* in association with avocado trees, but he did not specify the location or the variety or cultivar on which the observations were made. Reports of *H. elegans* boring in the inner bark of camphor trees (*C. camphora*) in Jamaica are common in the literature of the genus *Heilipus* (Fawcett 1906; Schwarz 1907; Rubio et al. 2009; Santos-Murgas et al. 2014); however, it is worth mentioning that they correspond to misidentifications of *H. mirus* (see above, genus *Cinnamomum*).

In Colombia, *H. elegans* is known to bore into the trunks of *P. americana* in its larval stage. In the Municipality of Fresno, Department of Tolima, Rubio et al. (2009) recorded damage by this species on both common or criollo trees and the cultivars Booth 8, Choquette, Lorena, Santana and Trinidad (Rubio et al. 2009). Additionally, in Colombia, larvae and adults of *H. leopardus* have been found inside the trunks of Hass avocado trees in the Municipalities of Urrao (Antioquia) and Manzanares (Caldas) (Díaz-Grisales 2019). In addition, 30 adults of *H. fassli* (Voss) that emerged from Hass avocado trunks in Urrao are housed at the MEFLG. This is the first report of the habit and host plant of *H. fassli*, which joins the list of *Heilipus* species that attack avocado in Colombia and shares the habit of boring trunks with *H. elegans* and *H. leopardus*. In Brazil, *H. catagraphus* larvae bore into the subcortical tissues of avocado (Bondar 1915; Costa-Lima 1956; Silva et al. 1968). Furthermore, *H. rufipes* larvae have been found in the trunks of avocado cultivar Bertanha in São Benedito, State of Ceará, Brazil (Lourenção et al. 2003). Finally, Silva et al. (1968) mentioned that *H. elegans* bores avocado branches and trunks in the State of Santa Catarina, Brazil. However, Vanin and Bená (2015) suggested that this information may correspond to a misidentification, since Wibmer and O'Brien (1986) did not mention the presence of *H. elegans* in Brazil in their South American catalogue.

Lineages in Lauraceae

Nine major evolutionary lineages in Lauraceae have been proposed by Rohwer (2000), Chanderbali et al. (2001), Rohwer and Rudolph (2005) and Song et al. (2017): *Hypodaphnis*, *Cryptocarya* group, *Cassytha*, *Neocinnamomum*, *Caryodaphnopsis*, *Mezilaurus* group, *Persea* group, Cinnamomeae and Laureae. The interactions recorded so far between *Heilipus* and 12 genera of the family Lauraceae occur in five of these nine lineages: Cinnamomeae (*Aiouea*, *Aniba*, *Cinnamomum*, *Damburneya*, *Mespilodaphne*, *Nectandra* and *Ocotea*), *Mezilaurus* group (*Clinostemon*

and *Mezilaurus*), *Persea* group (*Persea*), *Caryodaphnopsis* (*Caryodaphnopsis*) and *Cryptocarya* group (*Beilschmiedia*) (Table 1). Of the 33 Lauraceae species reported here as host plants for the genus *Heilipus*, 27 belong to the Cinnamomeae clade, two to the *Persea* group, two to the *Mezilaurus* group, one to the *Caryodaphnopsis* clade and one to the *Cryptocarya* group (Table 1). In terms of the number of *Heilipus* species, the Cinnamomeae clade occupies the first place with at least 15 associated *Heilipus* species, four trunk borers and the rest seed borers. The *Persea* group is the second lineage with more *Heilipus* species recorded, counting three seed borers and seven trunk borers. Four spermophagous species feed on the remaining three lineages: two species on the *Mezilaurus* group, one species on the *Caryodaphnopsis* clade and one species on the *Cryptocarya* group (Table 1).

Discussion

Heilipus as one of the main groups of pre-dispersal seed predators of Lauraceae in the Americas

The genus *Heilipus* has close ecological associations with magnoliids of the families Lauraceae (Laurales) and Annonaceae (Magnoliales). To date, the habits and host plants of 24 of the 90 species described in the genus are known, with information for four of these species being first reported in this study. Of these 24 species, 12 are seed borers and 12 are trunk borers. The trunk and branch boring habit could be considered more generalist, occurring in both Annonaceae and Lauraceae, whereas the seed boring habit is more specialised and exclusive to the family Lauraceae. With seeds of at least 30 species of Lauraceae in which the immature stages of *Heilipus* species develop, these weevils should be considered one of the most important pre-dispersal seed predators of this botanical family in the Americas. Although some authors assert that *Heilipus* larval feeding severely affects seed germination, especially if the embryo is damaged (Gómez and Toro 2007; Pessotto et al. 2021), the role of these weevils may not be entirely detrimental. Larval development of *Heilipus* species may facilitate seed germination, as observed by Sánchez-Garduño (1995) in *Damburneya ambigens* from Los Tuxtlas Region. In that case, seeds infested by *H. albomaculatus* germinated faster than those infested by *Pagiocerus frontalis* (Fabricius) (Curculionidae, Scolytinae, another pre-dispersal seed predator) and undamaged seeds (Sánchez-Garduño 1995). However, the fitness of seedlings derived from seeds where *Heilipus* completed metamorphosis without affecting the embryo remains unknown. Gómez and Toro (2007) noted that some seeds of *Aniba perutilis* not severely damaged by *Heilipus* larvae can germinate, but the seedlings soon die due to the lack of reserves. Unfortunately, this observation was not experimentally verified.

Oligophagy

The oligophagous feeding behaviour of *Heilipus* was documented by Díaz-Grisales et al. (2021), who reported that some species within the genus feed on plants from different genera of the family Lauraceae. This study expands on that finding, supporting that oligophagy is a very common pattern in this group of weevils, particularly amongst seed borers. Nine of the seed borers listed in Table 1 are associated with more than one host plant (*H. albomaculatus*, *H. draco*, *H. guttiger*, *H. lauri*, *H. longirostris*, *H. pittieri*, *Heilipus* sp. nov. VDG1, *Heilipus* sp. nov. VDG6 and *H. vividaensis*), while the others have been observed on only one. Amongst the 12 trunk-borer species whose host plants are summarised here, four are associated with more than one host (*H. catagraphus*, *H. gibbus*, *H. lactarius* and *H. squamosus*), while the remaining eight have been detected on a single plant species (Table 1). This does not imply that the species documented on a single host plant lack additional hosts; rather, it indicates a need for more biological and ecological data, both on labels and in publications. The labels of *Heilipus* specimens held in scientific collections often lack biological data.

Oligophagy in trunk borers

Amongst the trunk borers reported on more than one host are *H. gibbus* and *H. lactarius*, which specialise in *Annona* species. The remaining two species, *H. catagraphus* and *H. squamosus*, have been recorded on trunks of the family Lauraceae. Notably, the hosts of *H. catagraphus*, *H. lactarius* and *H. squamosus* include native or endemic plants, as well as economically important plants cultivated near to the former. This suggests that *Heilipus* trunk borers may colonise alternative plant species in response to the loss of their primary host. For example, the anthropogenic pressure on the Atlantic Forest of Brazil due to massive agricultural expansion, industrialisation and urbanisation (Ribeiro et al. 2011) may have driven *H. catagraphus* and *H. lactarius* to migrate from native or endemic plants to related cultivated ones. Alternatively, trunk borers could be simply responding to a strong attraction to volatile organic compounds emitted by related plants growing in monocultures (avocado or *Annona* crops). This attraction can result in oviposition and the development of immature stages in these alternative hosts, as has been observed in avocado crops in some countries of the Americas (see below).

Nonetheless, a strong attraction to an alternative host does not always result in oviposition or larval development. For instance, Lourenção et al. (1984) observed *H. catagraphus* adults feeding on young avocado fruits of the Fortuna cultivar in a commercial orchard in Barão Geraldo, State of São Paulo. However, no larvae or immature stages were found in the avocado trunks and the adults disappeared two months later without any control measures (Lourenção et al. 1984). Similar-

ly, Reis et al. (2018) recorded adults of *Heilus freyreissi* (Boheman), another member of the subtribe Hylobiina, feeding on tender lateral branches, central leaf veins, inflorescences, peduncles and young fruits of avocado trees (cultivars Margarida, Breda and Hass) planted in Rio Paranaíba, State of Minas Gerais. Despite these observations, the study does not mention the presence of larvae or immature stages within any tissue of the trees (Reis et al. 2018).

Oligophagy and avocado crops

Persea americana is a highly attractive and suitable host for *Heilipus* species, providing food for adults and appropriate tissues for oviposition and larval development. Currently, ten species of *Heilipus* are associated with avocado in the Americas: three seed borers and seven trunk and branch borers. The biology of the three seed borers was documented in the early 20th century (Barber 1912, 1919; Dietz and Barber 1920), with *H. trifasciatus* being the last reported in 1920 (Dietz and Barber 1920). In contrast, the incidence of avocado trunk borers has increased since *H. catagraphus* was recorded in Brazil by Bondar (1915). Subsequent reports documented *H. squamosus* in the United States (Wolfenbarger 1948), *H. rufipes* in Brazil (Lourenção et al. 2003), *H. elegans* in Colombia (Rubio et al. 2009) and *H. albopictus* in Mexico (Castañeda-Vildózola et al. 2010). The most recent reports are from Colombia and include *H. fassli* (first mentioned in this study) and *H. leopardus* (Díaz-Grisales 2019).

The increasing incidence of *Heilipus* species on commercial avocado crops can be analysed through interactions between native insects and non-native plants (Bezemer et al. 2014; Sunny et al. 2015; Tallamy et al. 2020). Although *Persea americana* is native to the Americas, with a natural distribution from Mexico to Peru (Téliz and Marroquín 2019), commercially developed avocado cultivars (e.g. Bertanha, Booth 8, Choquette, Hass, Fortuna, Fuerte, Lorena etc.) may act as non-native plants in regions where they are cultivated. The introduction of non-native plants can alter the landscape for resident arthropods by affecting the regional coverage or abundance of native plant species (Bezemer et al. 2014). The establishment of avocado plantations has led to the replacement of native vegetation in some countries. In Michoacán, Mexico, deforestation and forest fragmentation have accompanied the expansion of avocado crops, illustrating this phenomenon (Cho et al. 2021; Denvir et al. 2022; Saldaña and Cota 2022). In the absence of their native host and being oligophagous, native populations of *Heilipus* are expected to migrate to a confamilial host. Given its close ecological association with Lauraceae, cultivated avocado is a suitable congener. Moreover, the introduction of non-native plants that serve as a highly suitable host can cause native insects to shift their primary or native host (Bezemer et al. 2014). Avocado monocultures may provide concentrated, high-quality resources for native populations of *Heilipus*, compared to their native host plants. Consequently, the likelihood of novel interactions between *Heilipus* species and avocado crops in the Americas depends on the diversity of species confamilial to avocado in the region where it is planted, as well as the diversity of these weevils.

The recent findings of *H. fassli* and *H. leopardus* damaging Hass avocado trunks in Colombia are a good example of novel interactions. This damage, recorded over the last five years, coincides with a 105% increase in harvested avocado areas in Colombia, from 53,801 ha in 2018 to 110,183 ha in 2022 (FAO 2023). Three key factors explain the increasing incidence of avocado trunk borers of the genus *Heilipus* in this country: 1) Colombia is second in *Heilipus* diversity after Brazil (Díaz-Grisales et al. 2021), 2) it has a significant richness of Lauraceae with 20 genera and 261 species (Soler et al. 2020) and 3) it is one of the top five global avocado producers (Arias et al. 2021; FAO 2023). Colombia's case is crucial for understanding *Heilipus* trends in colonising new host plants and ranges. These weevils can even attack non-native Lauraceae plants, as seen with *Cinnamomum camphora* in Jamaica and *Cinnamomum verum* in Brazil and Trinidad and Tobago. For avocados, the high specificity of known seed borers (*H. lauri*, *H. pittieri* and *H. trifasciatus*) suggests that other spermophagous *Heilipus* species are unlikely to target avocado seeds. Instead, generalist species are more likely to infest trunks and branches, as noted by Díaz-Grisales et al. (2021). This aligns with the hypothesis of Tallamy et al. (2020) that insects with larvae feeding on well-defended plant tissues, such as seeds, are less prone to incorporate non-native plants into their diets compared to species whose larval development occurs on less defended tissues, such as wood.

Oligophagy in seed borers

The oligophagous behaviour of spermophagous *Heilipus* species may have evolved in response to the annual variation in fruit production amongst individuals and species of Lauraceae (Wheelwright 1986). In Los Tuxtlas Biosphere Reserve, Mexico, *Damburneya ambigens* exhibits cycles of low and high fruit production (Sánchez-Garduño 1995). A seven-year study in Monteverde, Costa Rica, revealed that most Lauraceae fruited abundantly in three non-consecutive years and produced relatively little fruit in the other four years (Wheelwright 1986). In Brazil, irregular fruiting was documented in *Aniba rosodora* in Manaus, Amazonas (Spironello et al. 2004; Morais et al. 2009). Similarly, Silva et al. (2000) observed irregular flowering and fruiting in *Ocotea catharinensis*, varying between trees and years in the Parque Estadual da Cantareira, São Paulo. *Heilipus* species are likely to colonise other Lauraceae fruits and seeds when their primary or closely-associated host has low or no fruiting periods. This shift may also occur if the primary host has been previously colonised by other more dominant pre-dispersal seed predators. The primary or closely-associated host of *Heilipus* species remains poorly defined.

Patterns of specialisation within the spermophagous guild of the genus *Heilipus*

The available evidence indicates two levels of specialisation at the generic level in *Heilipus*: specialist and generalist. Specialists feed on different plant species within the same genus, such as *H. albomaculatus* on *Damburneya* seeds and *H. lauri* and *H. pittieri* on *Persea* seeds. Generalists feed on plants from different genera within the family Lauraceae, including *H. draco*, *H. guttiger*, *H. longirostris*, *H. vividaensis*, *Heilipus* sp. nov. VDG1 and *Heilipus* sp. nov. VDG6. Notably, generalists tend to associate with genera from the same clade or lineage within Lauraceae (Table 1). For example, *H. albomaculatus*, *H. draco* (with one exception), *H. guttiger*, *H. vividaensis* and *Heilipus* sp. nov. VDG1 specialise in the Cinnamomeae clade, while *H. lauri* and *H. pittieri* specialise in the *Persea* group. This level of specialisation suggests that spermophagous *Heilipus* species may be evolutionarily predisposed to oviposit in fruits of a specific Lauraceae clade. Genera within the same Lauraceae clade may share *Heilipus* seed borers due to the similarity in fruit and seed traits important for oviposition.

This tendency to associate with a specific Lauraceae clade is not fulfilled in three cases: *Heilipus* sp. nov. VDG6, recorded in *Aniba* sp. (Cinnamomeae clade) and *Caryodaphnopsis cogolloi* (*Caryodaphnopsis* group); *H. longirostris*, associated with *Aniba* sp. (Cinnamomeae clade) and *Mezilaurus* sp. (*Mezilaurus* group); and *H. draco*, documented on 12 plant species from seven genera, all in the Cinnamomeae clade, except *Beilschmiedia tovarensis* (*Cryptocarya* group - *Beilschmiedia* complex). Data on *Heilipus* sp. nov. VDG6 and *H. longirostris* suggest these species have a less common or abundant host belonging to an underrepresented genus in Colombia (*Caryodaphnopsis* and *Mezilaurus*) and an alternative host with a wider distribution due to its greater diversity in the country (*Aniba*). Thus, *C. cogolloi* and *Mezilaurus* sp. may be the primary or closely-associated hosts for these *Heilipus* species, with associations with *Aniba* sp. occurring during low or no fruiting periods of their main host.

The occurrence of *H. draco* in *B. tovarensis* was documented by Downey et al. (2020), who assessed interactions between pre-dispersal insect seed predators and seven Lauraceae species in Barro Colorado Island (Panama) over a two-year period. They concluded that these interactions are not largely related to the phylogenetic distance and trait similarity between hosts, but are likely driven by the volume of fruit produced by each tree species. The relatively high abundance of *H. draco* on *B. tovarensis* seeds may be related to fruit availability, as suggested by Downey et al. (2020), but also to the dominance of *Pagiocerus frontalis* in the other Lauraceae included in the study. The dominance of *P. frontalis* over another species of the genus *Heilipus* (*H. albomaculatus*) was also documented in seeds of *Damburneya ambigens* in Los Tuxtlas Biosphere Reserve (Rodríguez-Sánchez et al. 2022).

Given these three discussed exceptions, the clade-level specialisation in the spermophagous species of the genus *Heilipus* must be considered speculative until more data on host plants are available.

A proposal for a centre of origin of the genus *Heilipus*

With 29 documented species, Brazil records the greatest diversity of the genus *Heilipus* to date (Clarkson et al. 2024; Sanz-Veiga et al. 2024). Of these, 13 species are found in the southern and south-eastern regions: *H. bohemani* Boheman, *H. catagraphus*, *H. comtus* Boheman, *H. crocopelmus* Boheman, *H. draco*, *H. gibbus*, *H. lactarius*, *H. parvulus*, *H. peplus*, *H. rufipes*, *H. tricolor* Perty, *H. velamen* and *H. vividaensis*. In the Amazon biome, *H. discoides* (Fabricius), *H. niveodecoratus* Lucas and *H. odoratus* are present. The distribution of *H. angusticollis* (Pascoe), *H. circulatus* (Pascoe), *H. hopei*, *H. luctuosus* Lucas, *H. nudipennis* (Pascoe), *H. osculatii* Guérin and *H. paradoxus* (Pascoe) in Brazil is uncertain, but they may also occur in the Amazon Region, based on the type localities and material examined from other South American countries. *Heilipus rufipes* has also been recorded from the central-western and north-eastern regions and *H. affinis* Guérin from the central-western region. Although *H. annuliger* (Latreille), *H. aulicus* (Pascoe), *H. empiricus*, *H. mirus* and *H. rugicollis* Boheman have been reported in Brazil (Wibmer and O'Brien 1986; Clarkson et al. 2024), the specific regions or States of their occurrence remain undocumented.

Brazil also hosts a great diversity of Lauraceae and Annonaceae, with 469 and 389 species, respectively (Flora e Funga do Brasil 2024). With 15 out of 38 records, it is the country with the highest number of reported host plant species for the genus *Heilipus* in the Americas and the only one where the trunk-boring habit has been recorded in both Annonaceae and Lauraceae. Thirteen of these 15 known host plants, both cultivated and native, are found in the southern and south-eastern regions of Brazil. Ten of them (*A. mucosa*, *A. muricata*, *A. reticulata*, *A. sylvatica*, *O. porosa*, *O. puberula*, *N. angustifolia*, *N. nitidula*, *O. catharinensis* and *P. americana*) occur in the Atlantic Forest phytogeographic domain (Flora e Funga do Brasil 2024), one of the two biodiversity hotspots in Brazil (Lobão 2017). It is possible that the centre of origin of the genus *Heilipus* is in the southern and south-eastern regions of Brazil, within the phytogeographic domain of the Atlantic Forest. Two main facts support this hypothesis: 1) nearly half of the *Heilipus* species recorded in Brazil and more than 60% of their known host plants are found in this phytogeographic domain (Flora e Funga do Brasil 2024) and 2) trunk-boring *Heilipus* species associated with both Annonaceae and Lauraceae, as well as seed-boring species associated only with Lauraceae, are present in the southern and south-eastern regions of Brazil, in one or more of the phytoecological regions that comprise the Atlantic Forest.

Conclusions

Compiling literature records is of great importance to complement data obtained from the study of material deposited in scientific collections. Integrating these information sources is essential for a comprehensive understanding of *Heilipus* and other weevil groups.

Additional records are required, since only the habits and host plants of 24 of the 90 species that comprise the genus are currently known. Given that most of the existing records originate from Brazil, Colombia, Costa Rica, Mexico and Panama, it is crucial to gather data from other countries, particularly those with a significant diversity of Lauraceae, as well as to conduct new field collections. To gain further insight into the biology of other *Heilipus* species, it is necessary to find developing larvae in the field and conduct rearing studies. Signs displayed by trunks and fruits may assist in the identification of infested plants.

Oligophagy is common amongst *Heilipus* species. Trunk borers may shift hosts due to the loss of their primary host or attraction to volatile organic compounds emitted by confamilial hosts in monocultures. These factors may explain the increasing incidence of *Heilipus* trunk borers in avocado crops across the Americas. For seed borers, host shifts may occur during low or no fruiting periods of their primary or closely-associated host or when more dominant pre-dispersal seed predators have previously colonised the primary host.

Gathered data suggest that *Heilipus* seed borers may be evolutionarily predisposed to oviposit in fruits of specific clades or lineages within the family Lauraceae. Nevertheless, they may exhibit some flexibility in host use beyond the clade level, making this hypothesis speculative until further evidence is available.

Detailed phylogenetic and systematic studies are required to elucidate natural lineages within *Heilipus* and to infer the probable feeding habits of closely-related species whose biology is unknown.

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Supplementary material 1

Specimens and literature

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